

FOSSIL PENAEIDAE (CRUSTACEA: DECAPODA) FROM THE
LOYOLA FORMATION, ECUADORRODNEY M. FELDMANN¹

Research Associate, Section of Invertebrate Paleontology

LUIS CHIRINO-GALVEZ¹GREGORY L. MASON¹JESSICA L. ANDERSON¹PATRICK W. DUNCAN¹REBECCA A. WARD¹DAVE R. SALEM¹

ABSTRACT

Specimens of fossil shrimp, preserved in the fine clastic sediments of the middle Miocene Loyola Formation, within the Cuenca Basin, Ecuador, have been identified as *?Penaeus maddeni* n. sp. Their presence strongly suggests that marine conditions existed within the basin during the deposition of some of the Loyola Formation and that the geological history of marine influence in Andean intermontane basins is complex. This observation is reinforced by the presence of claws of a crab identified as *?Necronectes proavitus* (Rathbun) from a nearby locality within the formation. Because the identification of the crab claws is questionable, their use as a stratigraphic index is more limited than previously suggested.

INTRODUCTION

The Loyola Formation consists of about 500 m of dominantly thin-bedded shale deposited during the middle Miocene in the Cuenca Basin of Ecuador. The unit is significant in that it contains a diverse assemblage of vertebrate, invertebrate, and plant fossils. Among these are numerous casts of penaeid shrimp that were apparently deposited in one or two brief events. The Loyola Formation is also significant in that analysis of its sediments and enclosed fossils can provide information on the geologic history of the Cuenca Basin. Depth, temperature, and salinity conditions within the basin at the time of deposition of the fossil shrimp can be deduced by analyzing the enclosing sediment using thin sections, SEM, and X-ray analysis in conjunction with interpretation of fossil material. The primary purpose of this paper is to describe the fossil shrimp remains and to present some observations on their implications for the geologic history of the Cuenca Basin.

¹ Department of Geology, Kent State University, Kent, Ohio 44242.
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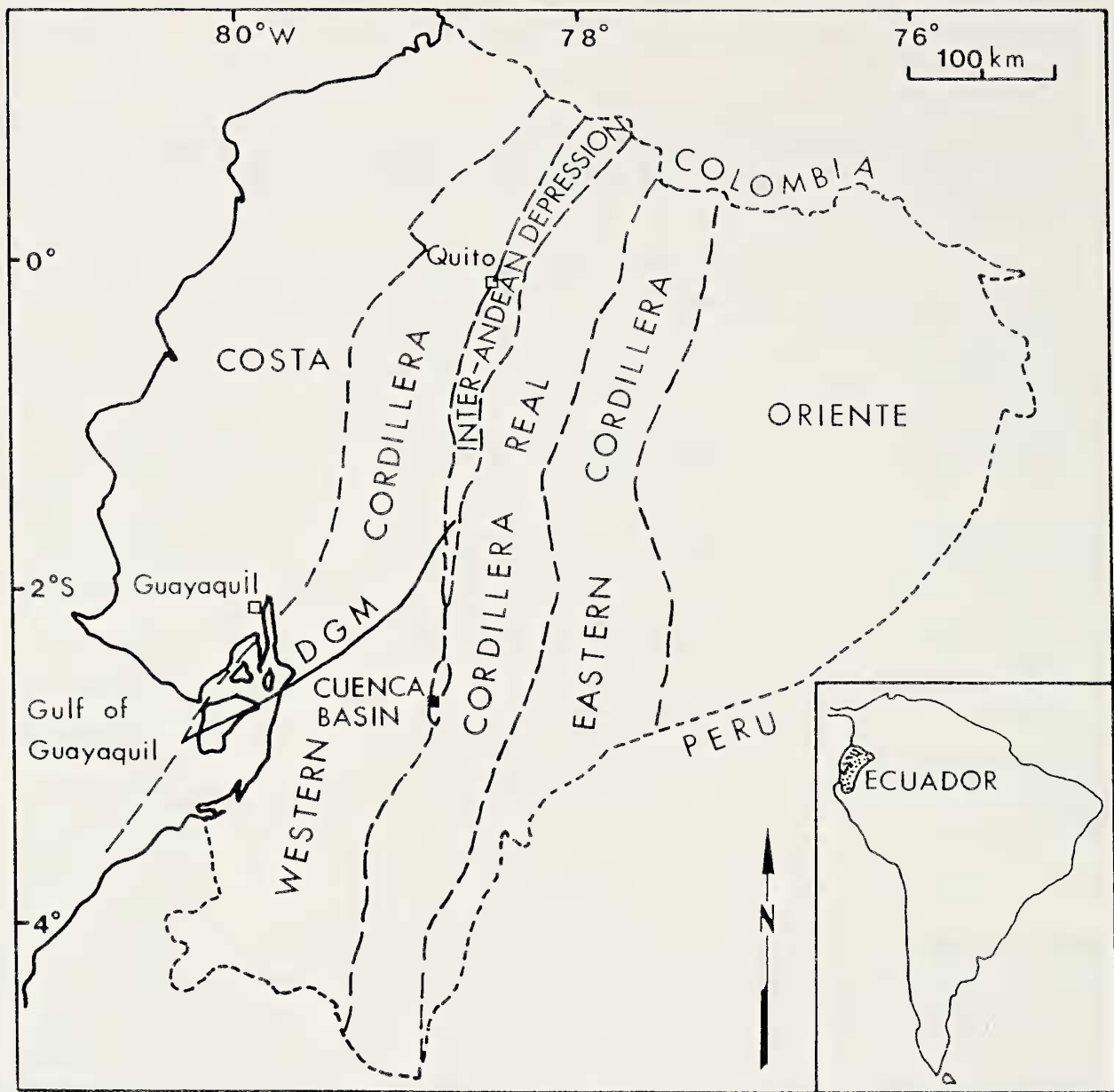


Fig. 1.—Generalized map of Ecuador showing the major tectonic regions referred to in the text (modified from Baldock, 1985). The southern trace of the Dolores-Guayaquil megashear (DGM) is superimposed from Megard (1989). Fossil shrimp were collected from the Cuenca Basin and the black square indicates the location of the larger scale geologic location map, Fig. 2.

REGIONAL SETTING

In no place are the northern Andes narrower than in central-southern Ecuador, the Sierra, where the average width is 100–140 km. North of latitude $2^{\circ}15'S$ the Andes are divided into two parallel ranges, the Cordillera Real and Eastern Cordillera to the east with peaks exceeding 4500 m, and a Western Cordillera separated by a continuous inter-Andean valley and the Cauca-Patia graben. South of latitude $2^{\circ}15'S$ the Sierra is more uniformly mountainous, with few peaks exceeding 4000 m. The Cuenca intermontane basin, lying within this region, is of Miocene age, and has been described as a strike-slip basin (Lavenu and Noblet, 1989; Fig. 1).

The northern Andes are a cordilleran orogen, whose western parts consist of accreted terrains of oceanic origin (Megard, 1989). The boundary (suture) between oceanic and continental crust is the Dolores-Guayaquil Megashear (DGM) (Fig. 1). The DGM follows approximately the Cauca-Patia graben and the inter-Andean valley in the north and bends southwest at approximately latitude $2^{\circ}S$ into the Gulf of Guayaquil and ends at a triple point in the Ecuadorian trench. To the east of the DGM suture is silicic crust of continental origin.

The Andean orogenic cycle began in Norian times, when the sea invaded extensive continental areas (Megard, 1989). In Lower Cretaceous times, under the influence of the great worldwide transgression, the Oriente of Ecuador, situated on what then constituted the western edge of the South American plate, became submerged to form a broad continental shelf which persisted through Santonian time (Feininger and Bristow, 1980).

The massif of the Proto-Cordillera Real of Colombia began to emerge during the early Tertiary, which was a period of deformation and/or uplift known as the Incaic phase of the Andean orogeny. In western Colombia and Ecuador, during the late Eocene to early Oligocene, diastrophism correlating with the Andean orogenic cycle affected the Sierra. This resulted in local folding, low-grade metamorphism and widespread plutonism (Baldock, 1985). Uplift and minor overthrusting along the Sub-Andean fault zone contributed to the rise of the Proto-Andes and the formation of intermontane basins, mostly of Miocene age. These include the Cuenca Basin of Ecuador.

Important changes occurred in western Colombia and Ecuador in Eocene time with the development of a sedimentary basin, the Bolivar Geosyncline of Harrington (1962). This basin was interposed between the rising Cordilleras and a foundered landmass to the west. The basin extended from the Gulf of Guayaquil northwards through Colombia and into the Caribbean. Marine sedimentation began in the south in the early to middle Eocene, gradually encroached northward and continued intermittently into the upper Miocene (Nygren, 1950). The Gulf of Guayaquil, "the Ecuadorian portal" or "Guayaquil portal" to this basin, is a transverse basin that forms a divide in the present drainage system and represents a deep portion of the major basin, the "Bolivar Geosyncline." The entire basin periodically served as a seaway during various times from Eocene to late Pliocene (Nygren, 1950).

In early Oligocene time the sea advanced through the Ecuadorian portal and reached the Oriente of Ecuador (Harrington, 1962). The upper Oligocene sea spread over great areas, extending as far east as the Cauca-Patia graben and throughout the length of the geosyncline with very low borderlands on the east and the west (Nygren, 1950). This seaway persisted, with continued shallowing, up to the lower middle Miocene.

During the upper middle Miocene, widespread volcanism occurred throughout the southern and central Andes (Hall and Calle, 1982). Increased orogenic movement was accompanied by faulting and igneous activity. The western border of the basin was down faulted beneath the Pacific and the eastern borderland raised into the high peaks of the Western Cordillera. The sea was then forced out, except in the deepest areas and the gulfs at each end (Nygren, 1950).

The area of the Gulf of Guayaquil apparently was more mobile than areas to the north and south. This mobility resulted in the opening of the Gulf, which probably began in the late Eocene. The Gulf of Guayaquil is a pull-apart basin resulting from the northward motion of the Western Ecuadorian Columbian Megablock along major longitudinal fault zones, like the DGM (Megard, 1989). During the pull-apart events many deep basins were formed which can be interpreted as fault blocks that were left behind.

During the Miocene, sediments were deposited within the intermontane basins in the progressively uplifted cordillera. Plutonism was widespread along the Western Cordillera. In the late Miocene, arching of the uplifted Sierra reintroduced a tensional regime that caused the development of the inter-Andean valley, bounded by reactivated normal faults.

The pull-apart of the Gulf of Guayaquil resulted in subsidence of the fault blocks that remained and creation of deep marine basins less than 75 km west of Cuenca. The area of the Cuenca Basin is bounded by many faults trending in a southwest to northeast direction. Reactivation of these faults during the Quenca 3 phase of the Andean orogeny may have resulted in subsidence of both the low Western Cordillera and the inter-Andean valleys, which were also being overthrust from the east by the Eastern Cordillera. The lower to upper Miocene age of the Loyola Formation, which was deposited in the Cuenca Basin, corresponds to the pull-apart of the Gulf of Guayaquil, marine invasion of the "Bolivar Geosyncline," and a global eustatic rise in sea-level estimated at 150 m (Hardenbol et al., 1982).

STRATIGRAPHY AND LITHOLOGY

There are seven recognized sedimentary formations within the Cuenca Basin (Fig. 2, 3). The oldest of these is Cretaceous in age. The basal relationship of the Cretaceous Yunguilla Formation is unknown (Bristow, 1973). The Miocene Biblián Formation is suspected to unconformably overlie the Cretaceous Yunguilla Formation supporting a depositional hiatus between the Cretaceous and the Miocene. In the depositional center of the basin, the basal contact of the Biblián Formation has not been explored to confirm this hiatus.

The Miocene Loyola Formation conformably overlies the Miocene Biblián Formation in the center of the basin and is exposed along the flanks of the Biblián Anticline and the Azogues Syncline. Toward the northeast margin of the basin, the Loyola Formation oversteps the Biblián to lie directly on the Yunguilla Formation. This may suggest a low stand of basin water allowing erosion along the shorelines prior to transgression and deposition of the basal beds, including the conglomerates, of the Loyola Formation. The fine-grained nature of the succeeding beds in the formation represents a period of maximum extent of the Cuenca Basin during the Miocene (Noblet and Marocco, 1989). This was a period of greatest likelihood for marine transgression into the basin prior to its closure.

The Loyola Formation consists largely of fissile gray to cream shales and silty shales with a conglomeratic unit at the base. Limestone lenses occur throughout, as do gypsum veins and coatings on joints and bedding planes (Bristow and Parodiz, 1982). Small beds (2–3 cm) of calcareous sandstones have been noted in the basal beds (Bristow, 1973). The thickness of the Loyola Formation has been estimated at 360 m, with the basal conglomerates comprising up to 45 m locally (Bristow, 1973). The basal conglomerates are well developed to the northeast, and appear to die out toward the center and southwest of the basin.

Other than fish remains and leaves, fossils are uncommon outside of the basal beds. The basal beds are, however, the most richly fossiliferous beds within the Cuenca Basin and have yielded 26 of the 33 species of bivalves and gastropods identified by Bristow and Parodiz (1982). Ostracods and molluscs occur in the basal sequence, with local shell beds composed almost entirely of *Doryssa bibliana* (Mollusca: Gastropoda) (Bristow and Parodiz, 1982). Echinoids have also been reported from the basal beds of the Loyola (Erazo Vallejo, 1965); but the whereabouts of the documenting specimens is not known and their presence has not been confirmed. Crustacean material, tentatively identified as *Necronectes proavitus* (Rathbun), is reported to be common in the basal sequence (Bristow and Parodiz, 1982). Thus, the fossils which have been identified previously from the basal beds would seem to indicate at least an initial marine condition during deposition of the Loyola Formation.

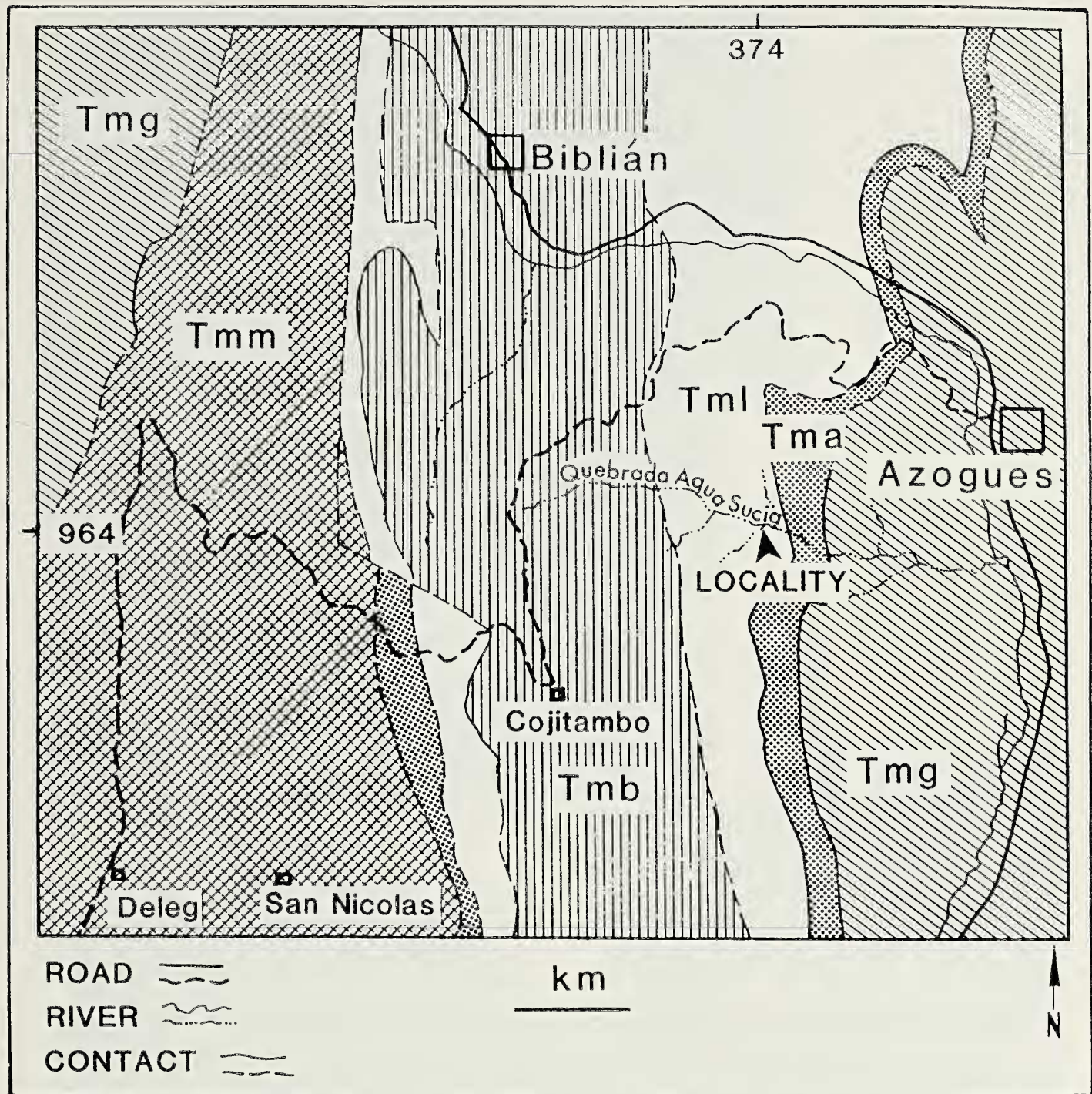


Fig. 2.—Geologic map of the region surrounding Azoges, Ecuador, from which *?Penaeus maddeni* n. sp. was collected. Tmb = Biblián Formation; Tml = Loyola Formation; Tma = Azoges Formation; Tmg = Guapán Formation; Tmm = Mangán Formation. Base map taken from the Azoges (1:50,000) quadrangle from the geologic map of Ecuador and provided by Dr. Richard Madden.

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1803
 Infraorder Penaeidea de Haan, 1849
 Superfamily Penaeoidea Rafinesque, 1815
 Family Penaeidae Rafinesque, 1815
 Genus *Penaeus* Fabricius, 1798
?Penaeus maddeni new species
 (Fig. 4, 5)

Diagnosis.—Very small penaeid with extremely thin cuticle, long rostrum with dorsal and, apparently, ventral spines; distinguished from other members of the genus by having relatively well-developed cervical groove, antennular flagellae

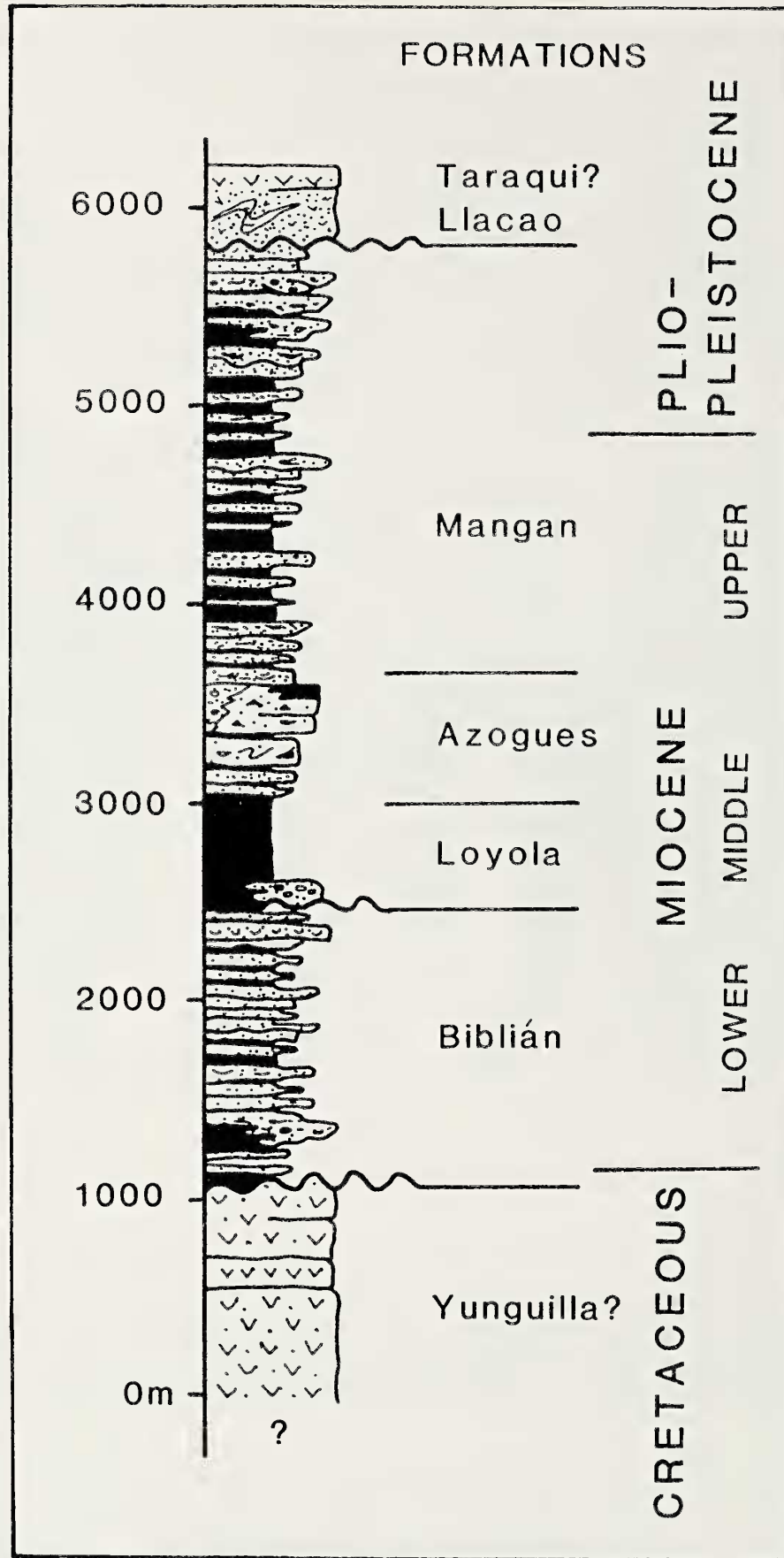
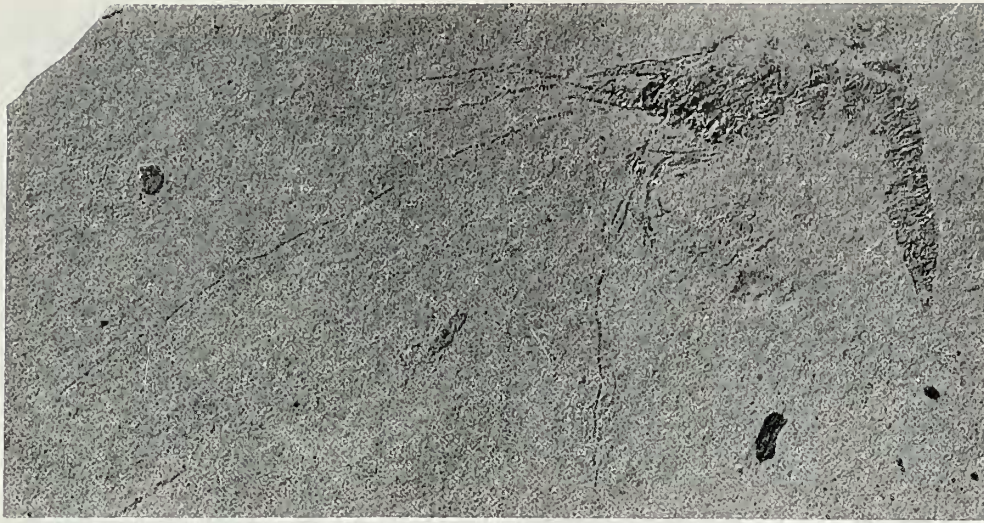


Fig. 3.—Stratigraphic section of rocks in the Cuenca Basin showing the distribution of coarse and fine clastic rocks in the Tertiary sequence (modified from Noblet and Marocco, 1989). Note that the Azogues and Guapán formations, as denoted on Fig. 2, are considered a single unit, the Azogues Formation, on this section.

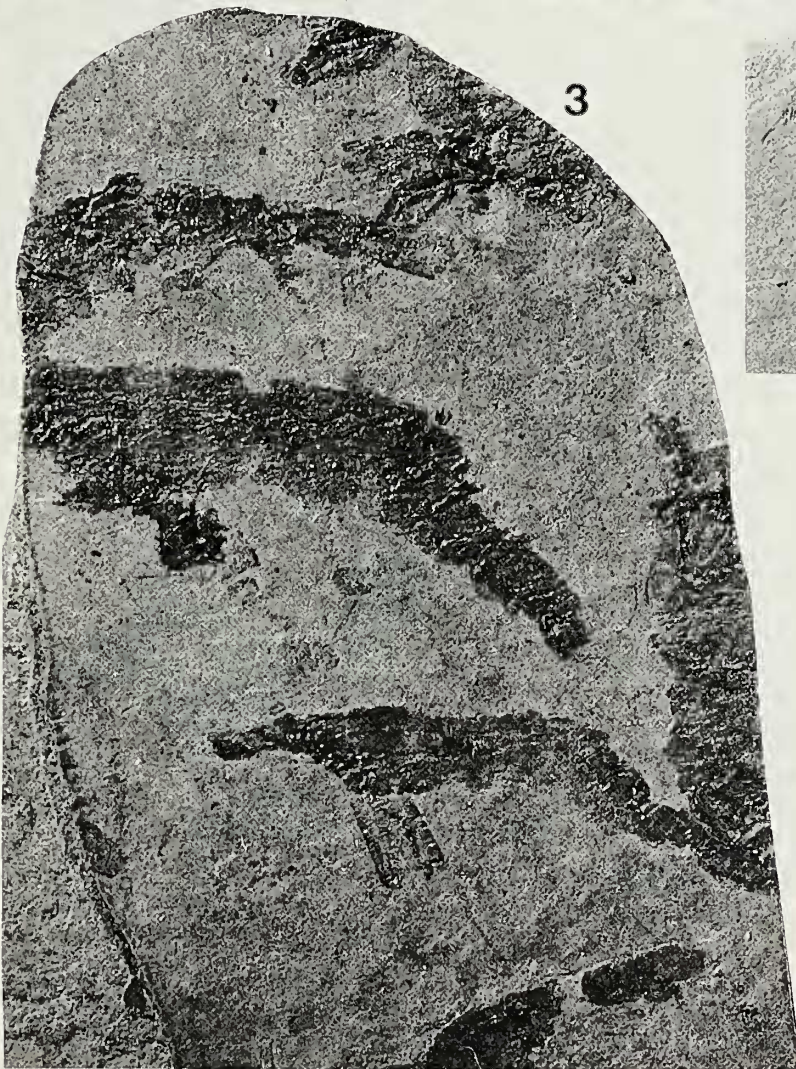
Fig. 4.—?*Penaeus maddenii* n. sp. 1, Left lateral view of holotype, CM 35820, showing the impression of the antennae and rostrum. 2, Right lateral view of paratype, CM 35821. 3, Six individuals, CM 35822, preserved on a bedding plane. Note the telson and uropods on the uppermost specimen. 4, Left lateral view of incomplete paratype, CM 35823, showing nature of thoracic appendages and detail of abdominal somites. 5, Right lateral view of paratype, CM 35824. Scale bar equals 1 cm.



1



2



3



4

5





longer than carapace; strongly reflexed abdomen with triangular pleurae on somites 1–5 and no overlap of pleuron 2 over that of 1 and 3.

Description.—Cephalothorax longer than high, smooth, apparently lacking spines in orbital region; rostrum about 70% length of carapace measured from base of orbit to posterior margin, uniformly tapering anteriorly, with at least three delicate spines along dorsum and indication of spines on venter, dorsal crest extending posteriorly to cervical groove; orbit small, well defined, eyes and eyestalks relatively short, extending to midlength of rostrum; cervical groove weakly expressed, crossing midline and extending ventrally approximately to level of base of orbit.

Abdomen smooth, uniformly tapering posteriorly, strongly reflexed around somites 2 and 3; abdominal somites 1–3 about equal in length and longer than somites 4–6; pleura of somites 1–5 triangular with ventrally directed, pointed terminations; pleuron of somite 2 not enlarged and not overlapping pleura 1 or 3. Telson tapering distally in lateral view to sharp termination.

Appendages poorly preserved. Antennal scales tapering distally, about as long as rostrum. Antennal flagellae at least four times length of carapace. Antennular flagellae nearly two times length of carapace. Thoracopods elongate, very slender, carried with meri directed anteriorly and distal elements curved downward and posteriorly. Abdominal appendages appear to be flattened and about as long as abdominal somites are high.

Measurements.—Accurate measurements of individual elements of the fossils cannot be made because crushing and distortion make it difficult to identify specific points of reference. Overall lengths of specimens vary from about 14 to 24 mm.

Types.—The holotype, CM 35820, and paratypes, CM 35821–35834, are deposited in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. Additional paratypes are deposited in the Geology Department, Escuela Politecnica Nacional (EPN), Quito, Ecuador.

Etymology.—The trivial name recognizes Dr. Richard Madden, Department of Biological Anthropology and Anatomy, Duke University Medical Center, Durham, North Carolina, for having collected the material and for making it available to the senior author.

Locality and stratigraphic position.—The specimens were collected from the Loyola Formation on the western flank of the Biblián Anticline in an intermittent stream bed called Quebrada Agua Sucia, locality DU-EPN(Q)-006, Grid reference 374964 on CT-ÑV-E1, Azogues (1:50,000) topographic quadrangle (Fig. 2). Their precise stratigraphic position is uncertain at this time.

Remarks.—The specimens forming the basis for description of this new species exhibit sufficient detail to confirm placement within the Penaeidae and suggest reference to *Penaeus*. The possession of an elongate, serrate rostrum, a generally smooth carapace and abdomen, and recurved abdomen, along with the lack of an enlarged, overlapping pleuron on the second abdominal somite define the familial placement. Although numerous fragments of legs are preserved, the placement and number of chelae cannot be determined.

The pleura tend to be well developed and are triangular which is typical of species of *Penaeus*. Poor preservation of the rostrum does not permit conclusive determination of whether or not the ventral margin of the rostrum is denticulate; however, the holotype has a well-developed rostrum with what appears to be at least one ventral spine. In this regard, the specimens more closely resemble *Penaeus* than they do *Trachypenaeus* Alcock, another genus common to modern waters of the west coast of South America (Méndez, 1981). General morphology

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Fig. 5.—Bedding plane exposing 12 specimens of ?*Penaeus maddeni* n. sp. showing the nature of the preservation of most of the specimens and the density of specimens on the fossiliferous surfaces, CM 35825. Scale bar equals 1 cm.

of the specimens is most like that of other members of the genus *Penaeus*. Dall et al. (1990:61) observed that "all of the genera [of Penaeidae] have a distinctive appearance or facies, which is difficult to describe, but may be readily recognized with practice." There does not appear to have been any strong ornamentation on the carapace and there are no unusual features such as enlarged or recurved rostral crests or extremely pitted, setose surfaces.

In general, the quality of preservation of fossil penaeids tends to be poor and there are few examples of the group, relative to groups characterized by more strongly calcified skeletons. Thus, it is difficult to make detailed comparisons with other species. The relatively long antennular flagellae, delicate rostrum, and moderately well-developed cervical groove may be taken as important points to distinguish this species from other members of the genus. Measurement of the absolute length of antennular flagellae is difficult, owing to the fact that the elements are broken and disarticulated; but there is no doubt that the flagellae exceed the carapace length. It is possible that the characters of antennular length, form of rostrum, and development of cervical groove are sufficiently important to warrant naming a new genus. However, the quality of the specimens is so poor that this action would be unwise.

The integument of these shrimps is extremely thin, and preservation has resulted in compression and severe wrinkling of the remains. Nonetheless, most of the specimens are preserved as whole animals so that it is probable that the fossils represent dead animals rather than molts. This observation, coupled with the observation that the fossils occur in large numbers, one specimen often overlapping another, on just one or two bedding planes, strongly suggest that all the individuals died and were preserved in a single event. Because shrimp regularly exhibit swarming behavior, the preservation of a large number of individuals cannot be taken as clear evidence of a mass mortality event.

The individuals are small by comparison with other adult representatives of *Penaeus*. Females of most extant species attain total lengths of more than 20 cm (Dall et al., 1990). Thus, it is possible that these fossils represent juveniles, rather than adults.

It is important to note that penaeids are confined largely to marine conditions (Glaessner, 1969:R426); however, most species exhibit juvenile development in estuarine conditions (Dall et al., 1990). The taxa most closely related to the penaeids which have fresh-water representatives are the Atyidae and the Palaemonidae. These families are members of the Caridea and are characterized by having a large pleural flap on the second abdominal somite which overlaps the pleura of the first and third somite. That is not the case in *?Penaeus maddenii*. Thus, the presence of this genus in the Loyola Formation argues strongly for deposition of at least part of the formation under marine or estuarine conditions.

Infraorder Brachyura Latreille, 1803
Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Genus *Necronectes* A. Milne Edwards, 1881
?Necronectes proavitus (Rathbun), 1918
(Fig. 6)

Remarks.—*Necronectes proavitus* was initially reported from the Loyola Formation by Bristow (1973) and that observation was republished by Bristow and Parodiz (1982). The species was neither described nor illustrated, but simply was included in a list of taxa collected from the unit. However, the species has special

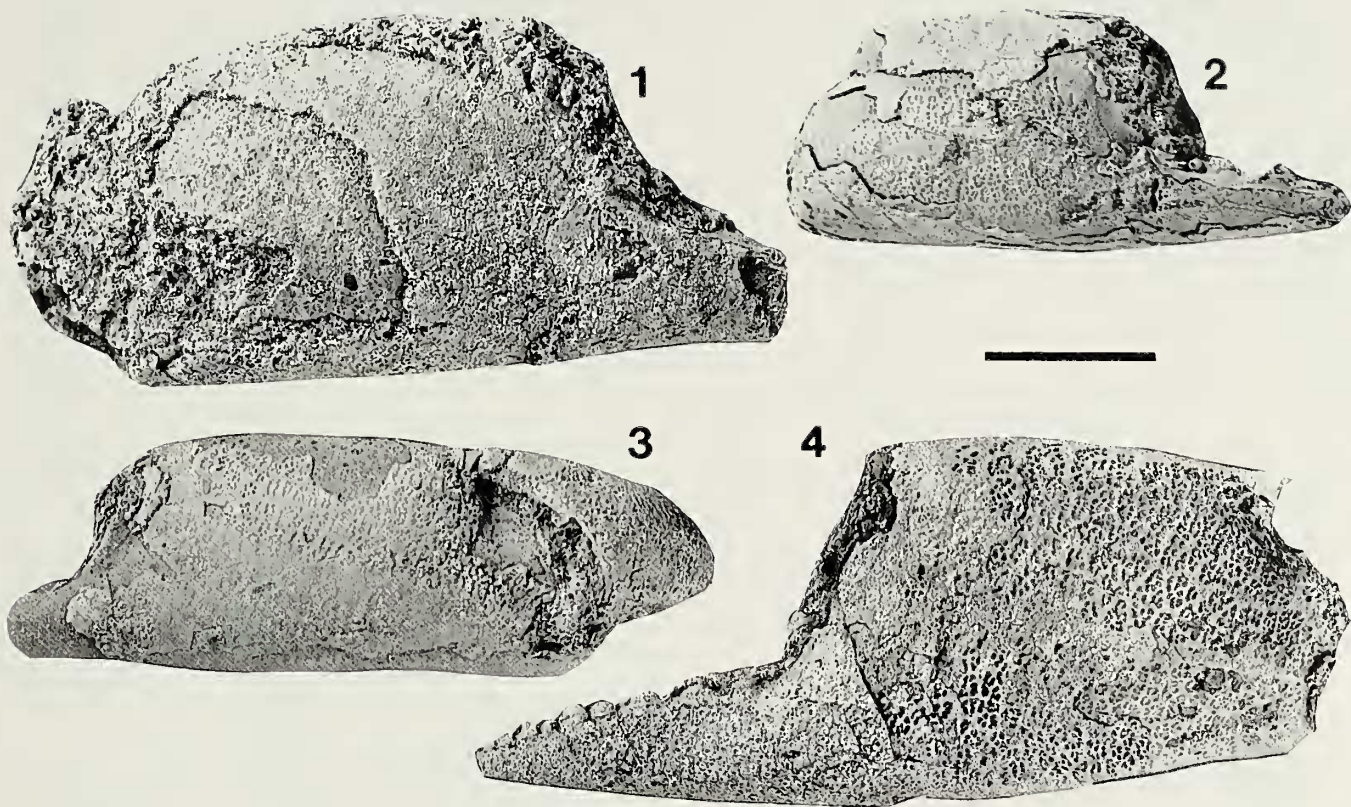


Fig. 6.—?*Necronectes proavitus* (Rathbun). 1, Outer surface of right cheliped, BMNH IN 61453. 2, Outer surface of right cheliped, BMNH IN 61454. 3, Outer surface of left cheliped, with attached carpus, BMNH IN 61455. 4, Outer surface of left cheliped, BMNH IN 61456. Scale bar equals 1 cm.

significance because it provided the best independent, paleontological evidence for the middle Miocene age of the Loyola Formation (Bristow and Parodiz, 1982: 11). In the original notice of the species, the identification was given as “. . . a form close to *Necronectes proavitus* (Rathbun) known only from the Miocene of Gatun” (Bristow, 1973:23). Thus, the establishment of the age of the Loyola Formation, based upon this species would have to be considered questionable. The subsequent reference to the species as an index to the middle Miocene (Bristow and Parodiz, 1982:11) gave no indication of the equivocal nature of the identification.

The material basis for this determination is 21 bits of claw material, including ten moderately complete hands and 11 fragments of carpi, fingers, and hands originally identified by S. F. Morris and now deposited in The Natural History Museum, London, under catalogue numbers BMNH IN 61453–61462. The material was collected from a single locality (Grid reference 404947) near the village of Antonio Borrero (also known as Charasol) (Bristow, 1973), about 5.5 km southeast from the locality at which the shrimp were collected. Re-examination of that material confirms that the specimens likely belong to a portunid or xanthid crab and that they are similar to those preserved on the holotype (Rathbun, 1918: pls. 55, 56) of *Gatunia proavita* Rathbun. However, firm identification of this species, based solely upon fragmentary claws, is not possible, so that although the specimens may be conspecific, the identification must be considered questionable. That being the case, the utility of the taxon as an index fossil must be questioned also.

LITHOLOGY AND DEPOSITIONAL ENVIRONMENT

Thin section analysis.—The rock in which the shrimp are preserved is a fissile, thinly laminated, brittle, silty shale, light grey on fresh surfaces and cream to light

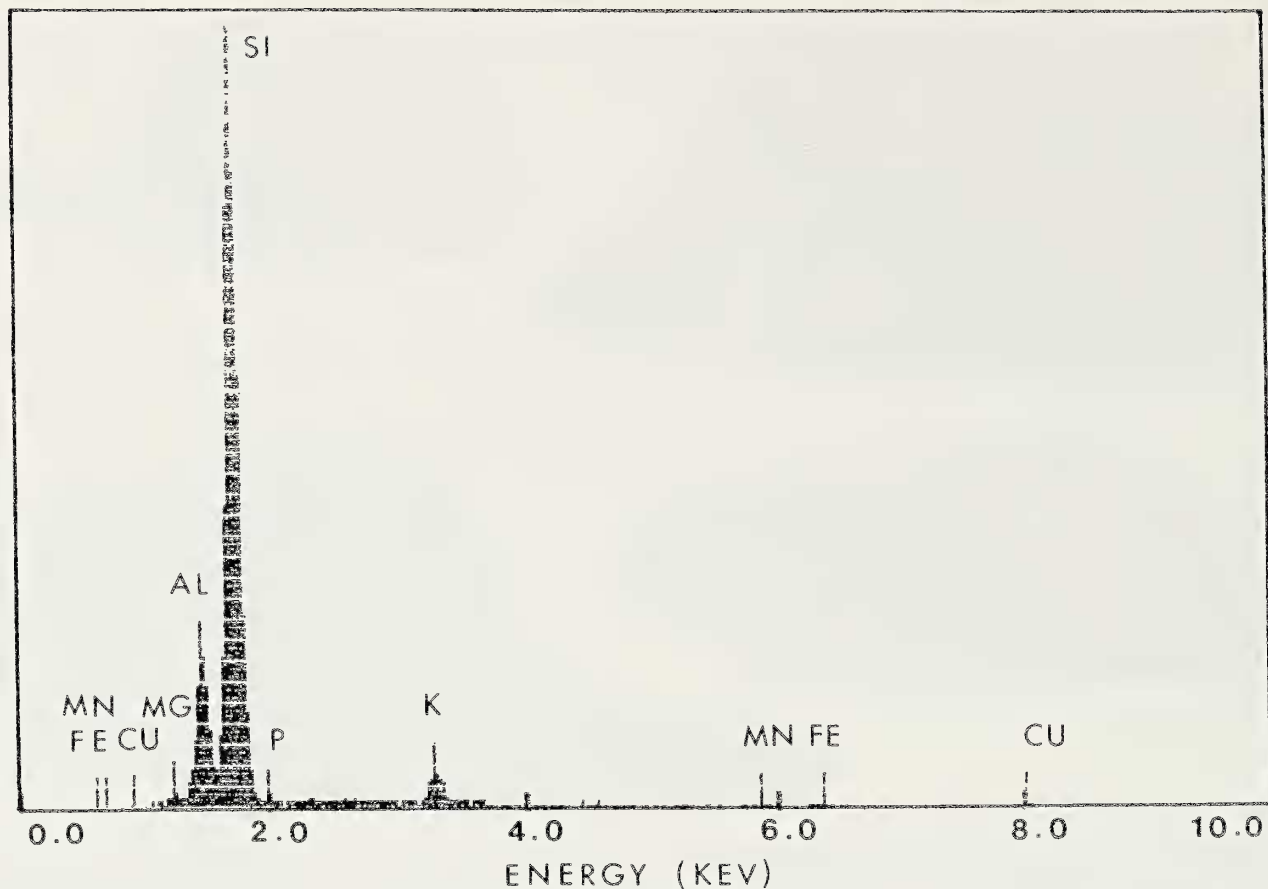


Fig. 7.—Energy dispersive X-ray pattern of sediment on bedding plane upon which *Penaeus maddenii* was preserved.

tan on weathered surfaces. Sedimentary structures, such as ripple marks or bioturbation, are generally lacking. In thin section, the silt-sized grains appear to be well-sorted quartz grains. Other constituents include clay minerals and minor feldspar grains. The rock is poorly cemented, moderately indurated, and lacks calcium carbonate either as grains or cement. The individual laminae, distinguished on the basis of faint variations in color, are laterally continuous, parallel to planes of fissility and typically uniform in thickness (10–20 laminae per cm), except where draped over fossils or larger grains. Fossils in the rock samples include fish scales, vertebral centra, and isolated bones (probably fish), in addition to the shrimp. Microfossils are apparently lacking in the specimen. The fossil shrimp are densely concentrated on one or two discrete bedding planes within the rock samples.

Whole rock SEM analysis.—Chemical analysis of the specimens from the Loyola Formation was conducted by means of an ISI SX40 scanning electron microscope and Princeton Gammatech energy dispersive X-ray attachment. Analysis was conducted using a high voltage source of 30 kV. Several analyses were conducted in order to obtain high point counts and consistent results. This analysis revealed the specimens to be composed largely of silica and aluminum, with minor constituents of potassium and copper (Fig. 7). The silicon, aluminum, and potassium concentrations are consistent with the presence of the mineral muscovite. Copper concentrations are consistently low; this element is thought to be a minor constituent which is bound up in the small clay fraction of the specimen. The rock exhibits an alternating sequence of organic and silicic mud layers. No significant compositional deviation was found between the fossiliferous layers and non-fossiliferous layers of the rock.

SEM analysis of chitin.—Original chitinous material was difficult to discern in

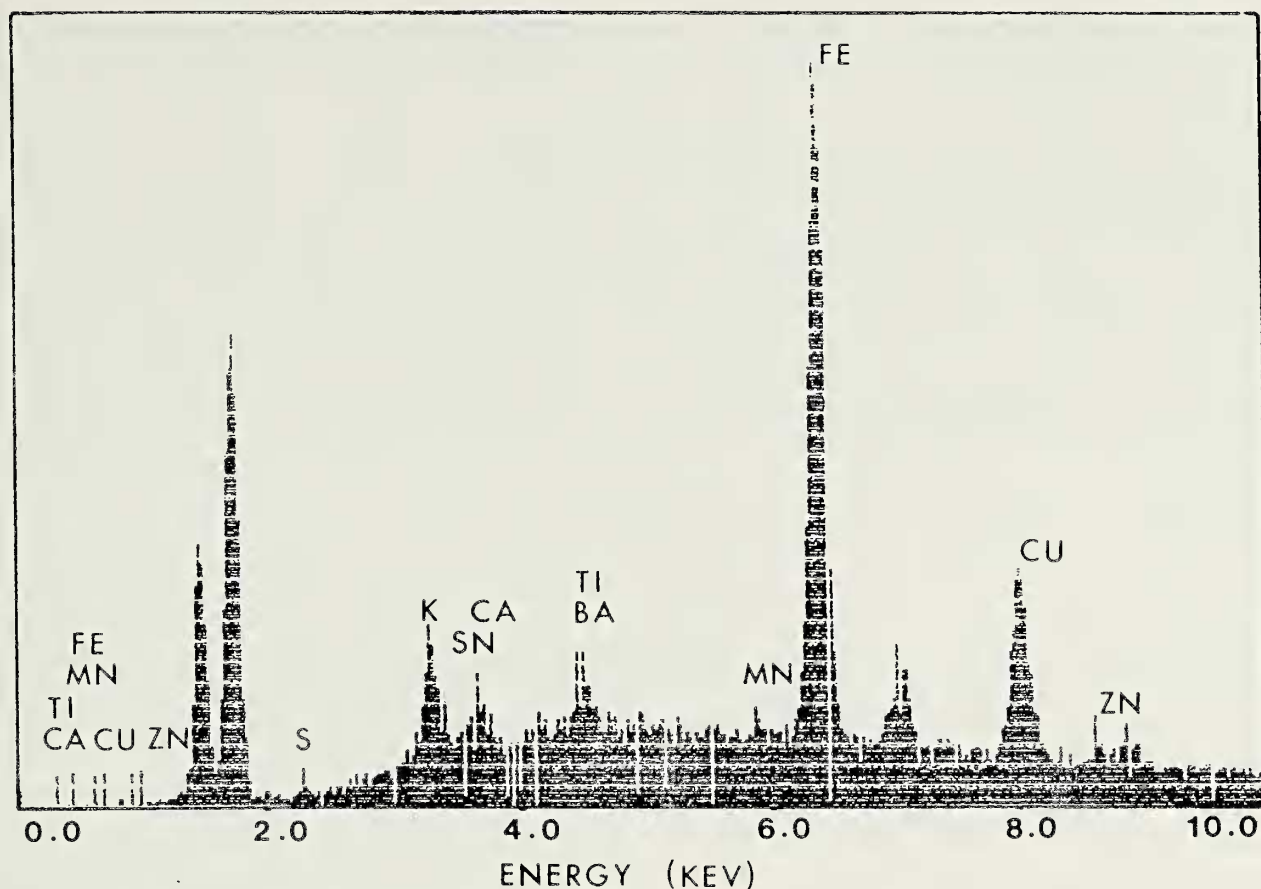


Fig. 8.—Energy dispersive X-ray pattern of cuticle sample from *Penaeus maddenii*.

the specimens under ordinary microscopic analysis. Nonetheless, material thought to be chitin from two different rock specimens was prepared for SEM/EDS analysis. Specimen #1 was less compressed than specimen #2, and had several thick (0.5 mm) sections of presumed chitin. Specimen #2 had been severely compressed and revealed abundant small filmy chitin remnants, some of which were very well preserved. Both specimens were analyzed repeatedly at 30 kV in order to obtain high point counts and consistent results.

EDS analysis of these samples revealed a concentration of trace metals and a background count higher than the rock samples. The most abundant constituents were iron and copper with minor amounts of zinc, nickel, and titanium (Fig. 8). Minute amounts of sulphur and calcium were also detected. Trace amounts of potassium were detected, but could not be separated from whole-rock composition.

ENVIRONMENTAL INTERPRETATION

General.—Analysis of the grain size, sorting, the uniformity in the range of sediment coloration, the lack of sedimentary structures, and the low degree of disarticulation of fossils in the rock samples support an interpretation of low energy conditions during deposition. The fine-grained nature of the bulk of the samples is indicative of a region of low depositional energy. The observed uniformity of coloration and the high degree of sediment sorting (uniformly fine grained) of individual layers is also indicative of very low energy conditions. The high degree of articulation of the fossilized shrimp remains would seem to indicate preservation under low energy conditions. If high energy conditions had prevailed, the remains would show a much higher degree of disarticulation due to reworking by wave or current action.

Depth.—The progression from sandstones and conglomerates directly into shales,

with no apparent break in deposition, is interpreted to be the result of marine incursion through the Gulf of Guayaquil, "the Ecuadorian portal," due to basin subsidence and sea level rise. Basin depth is controlled by subsidence. As the Loyola Formation approaches 360 m in thickness, subsidence could have equalled, or exceeded, that value. However, it is probable that much of the formation was deposited in a lacustrine setting, rather than a marine environment as is postulated for the lower part of the formation. If that is the case, subsidence and, therefore, maximum depth of deposition would have been less than 360 m. The sediments lack sufficient depth-indicating material, such as calcium carbonate, strontium, magnesium, and iron, to permit making a quantitative estimate of depth. In a qualitative sense, deposition of the shrimp-bearing beds occurred at a depth below wave base and above 360 m.

The alternating sequence of organic and silicic mud layers suggests shallow water deposition near an active source of siliciclastic sediment. The presence of silt grains in the silicic laminae precludes deposition beyond the reach of fluvial sediment, and the nature of the laminae suggests a low energy environment. Schram (1986) noted that most *Penaeus* were benthic inhabitants of shallow water which is consistent with a depth between wave base and 360 m.

Temperature. — Estimation of paleotemperature can be made using comparisons of temperature limitations of extant taxa related to those in the Loyola Formation, determining isotopic ratios of oxygen or carbon isotopes in suitable materials, or considering the paleogeographic setting in which the rocks were deposited. In this specific instance, only the latter approach is useful. The taxa found in the Loyola Formation and whose temperature range is known, *Diplodon* sp. and *Dorissa* sp., have rather non-restrictive temperature ranges (Camacho, 1966). The sediments lack calcium carbonate suitable for isotopic analysis. Thus, it is not possible to use analytical techniques on this material to determine paleotemperature. However, an estimate of high water temperature can be made based upon the equatorial position of Ecuador during the Miocene. A minimum temperature range of 25–28°C and be postulated for the surface water (Schopf, 1980). This range represents a minimum value because those are the temperatures of the open sea surface. A partially enclosed basin, such as the Cuenca Basin, most likely was even warmer.

Salinity. — The intermontane basins of the Sierra are characterized throughout the literature as "fresh water basins" (Bristow and Parodiz, 1982; Baldock, 1985). However, this is not consistent with the occurrence of ?*Necronectes proavitus*, a marine crab (Bristow and Parodiz, 1982), and echinoid fragments (Erazo Vallejo, 1965) in the basal Loyola Formation. Penaeid shrimp also are confined to marine conditions (Glaessner, 1969). Thus, while the majority of the taxa of the Loyola Formation may be fresh water organisms (Bristow and Parodiz, 1982), the marine component strongly argues for deposition of some of the formation under marine conditions. Additional stratigraphic control is necessary to determine the precise relationship between the marine and nonmarine components.

ACKNOWLEDGMENTS

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suggested that the specimens, if penaeids, might represent juveniles. Our sincere thanks to these people. Contribution 546, Department of Geology, Kent State University, Kent, Ohio 44242.

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